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Climate and wood quality have decayer-specific effects on fungal wood decomposition

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ABSTRACT

Any process that affects wood decomposition and decomposers in boreal forests may also affect the role that dead wood has on global carbon storages. We investigated under controlled laboratory conditions the impact of three major variables – temperature, humidity and wood quality – on Scots pine wood decomposition by four different fungal species. To reveal these effects, we conducted a nine-month factorial experiment. Wood quality was found to have a much more pronounced effect on fungal wood decay than climate variables. Furthermore, the fast-grown pine wood from managed forests decayed much faster than centuries old 'kelo' pine trees from natural forests as well as the slow-grown wood from managed forests. We found an overall increase in decomposition with temperature and humidity in *Gloeophyllum protractum*, except that the decay rate of the fast-grown wood declined with increasing temperature at higher humidity levels. The overall decomposition rates varied greatly with decayer species and wood type, and several interactions between temperature, humidity and wood quality effects were documented. In particular, we found that the fast decayers, *Dichomitus squalens* and *Fomitopsis pinicola* did not show any response to climate variables, but responded to wood quality only. The slow decayers *Antrodia xantha* and *G. protractum* responded to wood quality and interaction effects of climate and wood quality. Our results demonstrated species-specific effects of climate and wood quality when tested simultaneously, and show that it is critical to understand the different and complex mechanisms that affect wood decomposition and, consequently, carbon storages in forests, in order to increase the reliability of the climate-carbon prediction models.

1. Introduction

Boreal ecosystems, which contain approximately one-third of all remaining global forests, are an important storage of carbon (C) (Myneni et al., 2001; Bradshaw et al., 2009). Forests store C in several ecosystem components, including dead wood. The amount and continuity of dead wood is an integral component of forest ecosystems (Siitonen, 2001). Dead wood comprises of fine (FWD; 1–10 cm diameter) and coarse woody debris (CWD; diameter > 10 cm). High volumes of CWD, which mainly includes standing and fallen dead trees and stumps (Pregitzer and Euskirchen, 2004), has been associated with the occurrence of several red-listed forest species (Siitonen, 2001). The volume of CWD in natural forests can be up to 25–30 times more than in managed forests (Siitonen et al., 2000).

Climate change and warming is projected to have a significant impact on the boreal forests of northern Europe, particularly Fennoscandia (Kirschbaum and Fischlin, 1996; Christensen et al., 2007), as many of the ecosystem processes, as well as the growing season, are closely dependent on temperature (Christensen et al., 2007; Kellomäki et al., 2008). Climate change is predicted to bring about an increase in mean annual temperatures and precipitation (Christensen et al., 2007), a prolonged growing season, shorter snow season (Keller et al., 2005; Räisänen and Eklund, 2011) and increased forest productivity (Bergh et al., 2003; Kirilenko and Sedjo, 2007; Medlyn et al., 2011). Concurrently, climate change is also estimated to enhance microbial processes (Allison and Treseder, 2011) which are typically constrained by long periods of sub-optimal temperatures and low nutrient availability in boreal condition (Trumbore, 2009). This leads to stimulated soil organic matter decomposition due to soil warming (Bronson et al., 2008). In short, the likely increase in net primary productivity induced by warming may not imply an increase in net C storage. Rather,

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there is a risk that boreal forests turn from C sinks (Liski et al., 2003) to sources (Lindroth et al., 1998; Cox et al., 2000), which could initiate important climate feedbacks (Bonan et al., 1992; Allison and Treseder, 2011).

The decomposition of dead woody biomass is mostly affected by the activities of decomposer fungi (Boddy, 2001; Stenlid et al., 2008). Fungi are known to respond to environmental drivers, such as temperature (A'Bear et al., 2013) and humidity (Allison and Treseder, 2011), habitat quality (Gange et al., 2007; Lonsdale et al., 2008) and substrate quality (Edman et al., 2006) which can thus directly affect the decomposition process and boreal C cycling. For example, different moisture and temperature conditions, the long autumn season or the lack of snow cover in winter may directly affect the rate of annual decomposition and production of sporocarps (Gange et al., 2007; Piao et al., 2008). However, different functional groups of fungi are expected to have different responses to these environmental changes (Crowther et al., 2014).

Substrate quality (characteristics of dead wood) is still another factor that has a major influence on the fungal decomposition (Renvall, 1995; Edman et al., 2006; Tikkanen et al., 2006). Wood quality such as ring width, density and wood chemical composition vary depending on factors such as tree growth (Bouriaud et al., 2004), climatic factors (Briffa et al., 2002) and site fertility (Edman et al., 2006; Raiskila et al., 2006). This in turn may influence the decomposers that are substrate-dependent, and, thereby, affect the decomposition rates (Edman et al., 2006). Very few studies, however, have assessed how the decomposition processes differ between forest ecosystem types (in this case, natural vs. managed). Natural forests offer a high variety of woody substrates of which many are rare or even absent in managed forests. One good example is the '*kelo*' tree in boreal forests. Kelo is a Finnish term (which has been adapted to be used in English text as well) denoting very old Scots pine (*Pinus sylvestris* L.) trees that have grown slowly toward the end of their lives, gradually losing vigor and then dying slowly over several decades or even centuries while still standing. The seemingly higher decay resistance of kelo compared to normal Scots pine trees, which could be attributed to differential physical and chemical wood composition, is reflected in the number of rare saproxylic species that grow exclusively on, or strongly favor kelo trees (Niemelä et al., 2002). Kelos are quite unique in their appearance, and subtle differences in their wood quality (e.g. heartwood phenolic composition) with Scots pine wood from managed stands have been detected by Venugopal et al. (in press). This may influence wood decomposition rates, and one possible explanation for the differences in wood quality might be the slow tree growth of the trees that formed kelos.

There are gaps in our understanding of how current environmental changes will influence C accumulation in boreal forests and the principal ecological mechanisms related to these phenomena (Bradshaw et al., 2009). These questions are crucial as to how forests and their C stocks can be managed to aid in the mitigation and adaptation to climate change. In this study, we have simultaneously considered the effects of temperature, humidity and substrate quality along with their interactions on the fungal decomposition of boreal coarse woody debris, using different wood-decaying fungi. With an experimental approach we tested the following hypotheses which is illustrated by Fig. 1 with the etters (marked in red[1]) indicating the main research questions and their relationship to wood decomposition as addressed in this study:

[1] For interpretation of color in Fig. 1, the reader is referred to the web version of this article.

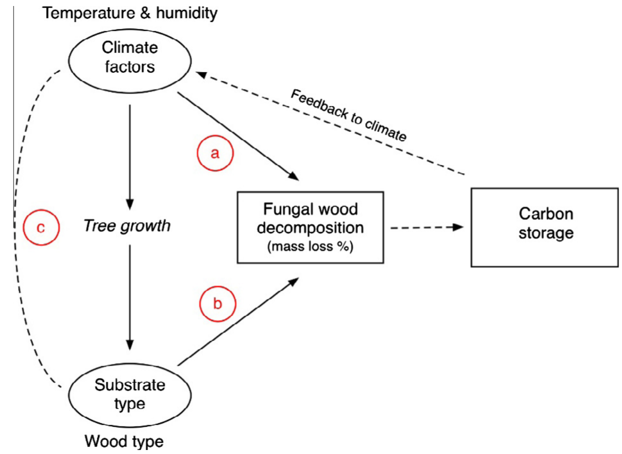

Fig. 1. Schematic illustration of relationships between climate variables, decomposer communities and the substrate quality. The letters a, b and c circled indicate the main variables and their interactions or relationship with fungal decay studied in this paper.

(I) Decomposer activity is strongly influenced by temperature and humidity factors (Allison and Treseder, 2011). Hence, we expect that an increase in temperature and humidity will lead to a higher overall wood decay rate which leads to the question of the direct impact of climatic factors on decomposition (Fig. 1a).

(II) Different saproxylic species are often quite specialized to particular substrates (Niemelä et al., 2002), which possibly reflects their effectiveness in extracting resources from woody material. If this is the case, wood decay rates will differ depending on the decayer species, although their ability to degrade wood of different qualities will vary. This leads us to the question of the direct effect of different substrate types on decomposition (Fig. 1b).

(III) Wood quality matters in decomposition (Edman et al., 2006; Cornelissen et al., 2012). Based on the decay-resistance observed in some slow-grown tree types – such as kelos – we predict that wood from fast-grown trees will decay faster than wood from slower grown trees. If this is confirmed, it may suggest that a climate driven increase in tree growth rate may result in a positive climate-C feedback through increased decay rates. This leads us to the question of how the climatic factors indirectly affect the fungal decomposition by modifying the substrate quality through tree growth (Fig. 1c).

Thus, in short, we hypothesize that different saproxylic fungi will exhibit differential wood decay rates that will vary with climatic conditions and wood quality. If this was the case, it would indicate that carbon storage and decomposition scenarios in many models, which assume uniform climatic and substrate-response from boreal fungal decomposers, need adjustments.

2. Methodology

2.1. Overview

To test the above hypotheses, we allowed four saprotrophic basidiomycete fungi to decay Scots pine (*Pinus sylvestris* L.) wood of three different qualities under different climatic conditions (Fig. 2). We focused on Scots pine as it is one of the principal Fennoscandian boreal tree species. Wood qualities in this study included fast- and slow-grown wood cut from fresh stumps after